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RESTING POSTURES OF ORB-WEAVING ULOBORID SPIDERS (ARANEAE, ULOBORIDAE)

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ABSTRACT

Observations of 22 orb-weaving species of the family Uloboridae show that these spiders assume one of four basic resting postures as they hang beneath the web's hub. The primitive pattern found in *Tangaroa* and *Octonoba* is characterized by all legs being spread and about equally flexed, whereas in *Zosis* the protracted first legs grasp the web at nearly the same point. *Uloborus* species typically assume a more cryptic posture characterized by acutely protracted and flexed first legs. Dense setal tufts proximal to the abruptly flexed leg segment provide outline camouflage and conceal the extended, shorter second legs which no longer support the body. In contrast, *Philoponella* species lack leg tufts and assume a compact posture with first legs folded against the sternum and only the last three pairs of legs grasping the web. The significance of these findings for uloborid classification and phylogeny is discussed.

INTRODUCTION

We have observed species in the orb-weaving uloborid genera *Uloborus, Octonoba, Conifaber*, and *Philoponella* in the field, and *Tangaroa* in captivity. The postures they assume while hanging from the hubs of their webs during the day are generally consistent within genera and in many cases differ between them. Thus these behaviors may be useful for field identification of uloborid genera, analysis of intrafamilial phylogeny, evaluation of the family's present generic division, and understanding the functional significance of differences in morphology.

With the exceptions of studies of *Hyptiotes* (Marples and Marples 1937, Peters 1938, Wiehle 1927, Wilder 1875) and *Miagrammopes* (Akerman 1932, Lubin et al. 1978), uloborid resting postures have received little attention. This is surprising in view of the striking differences that appear in early illustrations of these spiders. For example, the

crouched posture of *Philoponella (= Uloborus) republicana* shown by Simon (1891) contrasts with extended postures of *Zosis (= Uloborus) geniculatus* and *Uloborus glomosus (= U. americanus)* illustrated by Comstock (1913). Wiehle (1931) illustrates comparable contrasts in the postures of *Polenecia (= Sybota) producta* and an unidentified Central American *"Uloborus"* species which, judging by its resting posture, was a *Philoponella.* Eberhard (1973) concluded that the extended posture of *Uloborus diversus* represented an adaptation for concealing the spider since it was abandoned at night when the spider rested at the hub with all eight legs spread. It is surprising to find several postures among genera that all rest at the hubs of more or less horizontal orbs, particularly when their body shape and prey capture behavior are similar.

Most specimens upon which these observations are based are deposited in the Museum of Comparative Zoology, Harvard University. Representatives of *Tangaroa, Octonoba,* and some *Uloborus* and *Philoponella* are in the first author's collection.

OBSERVATIONS

Although we have observed four basic resting postures, all species studied for any length of time *(U. diversus, U. glomosus, P. semiplumosa, P. republicana,* and *P. vicina)* show some degree of variation. For instance, *P. vicina* sometimes rested in postures A and B, but when "disturbed" usually assumed posture D. *Uloborus diversus* usually rested with legs I and II extended anteriorly and touching each other, but sometimes one or both of legs II held the web and were not in contact with the others, or one leg I was not pressed against the other. These variations were particularly common after a spider had spread its legs and jerked its web in response to the impact of a prey (i.e., had assumed posture A), then failed to completely resume its usual resting posture. Additionally, postures A and B are not always easily distinguished as they differ only in the amount of separation between the first legs. The following descriptions are thus of stereotyped, "typical" postures which spiders often but not always assumed.

Posture A.—Figures 1-4. The spider rested with all eight legs spread and partly extended with each grasping a hub thread.

Posture B.—Figures 5, 6. Legs II, III, and IV were spread and partly extended to grasp web threads. Legs I were both directed nearly straight forward to grip the web and were only slightly separated along their prolateral surfaces. Legs I were flexed only slightly at the femur-patella and tibia-metatarsus joints.

Posture C.—Figures 7, 8. Legs I and II were pressed together and extended directly forward. The tibia-metatarsus joint of legs I was held at approximately 90°, while the tibia-femur angle was relatively small (15-25°) but more variable. Legs II were held tightly against the retrolateral margins of legs I, but their metatarsi and tarsi were only slightly flexed and, instead of gripping the web, the tarsi rested together in a crypt formed by dense setal brushes on the distal surfaces of the first tibiae. Legs III and IV held the web and were held close to the abodomen.

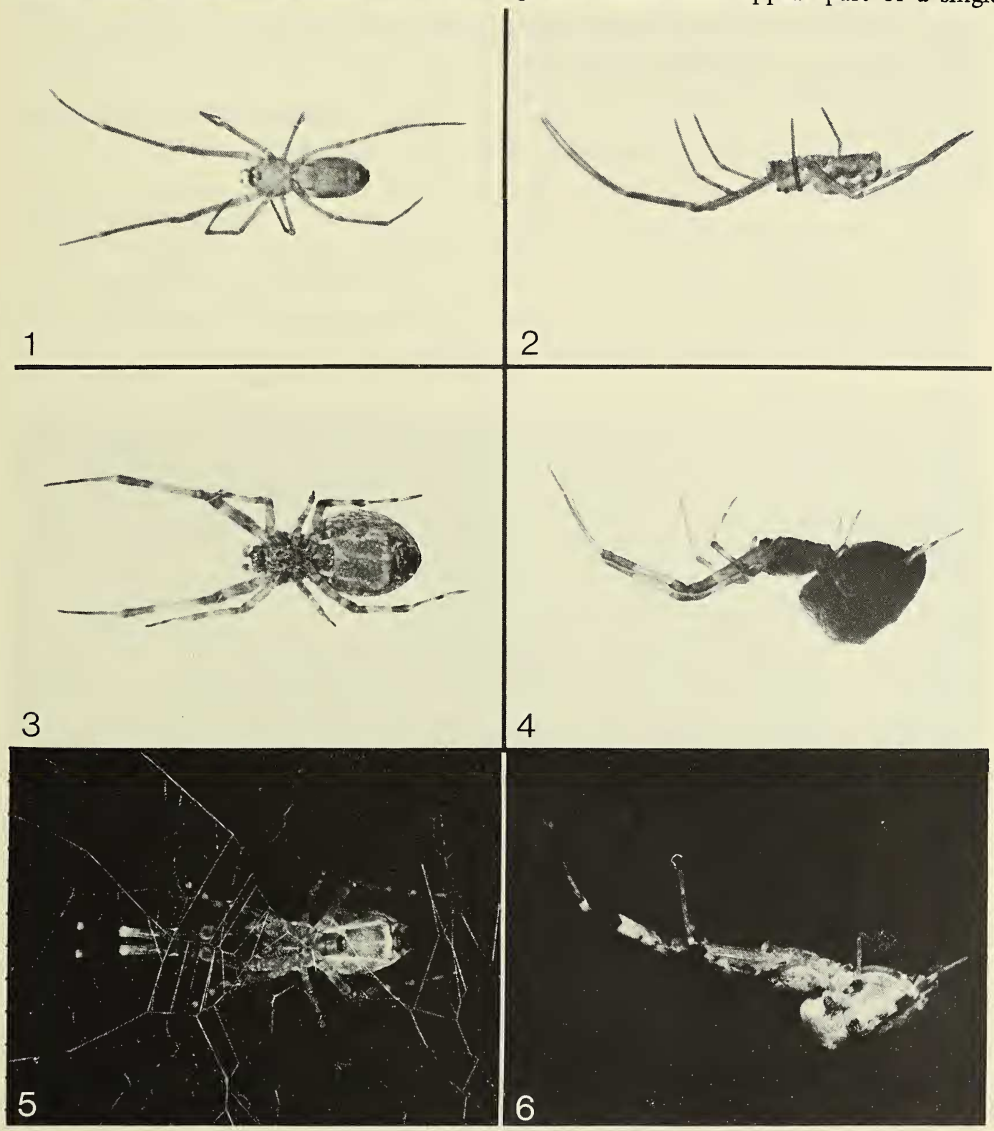
Posture D.—Figures 9, 10. The first legs were folded so that the tarsi and metatarsi were ventral to and nearly parallel with the sternum, and their tarsi did not grip the web. Legs II were also held flexed, with the femur forming a about 90° angle with the plane of the sternum; the femur-tibia angle was about 45°, the tibia-metatarsus angle about 90°, and the tarsal claws gripped the web. Legs III and IV also held the web and were pressed against the lateral surfaces of the abdomen. In at least one species (*Uloborus* 2072) the tip of the spider's abdomen projected upward and apparently pushed the web above it

into a small dome (similar behavior occurs in the araneid genera *Mangora, Mecynogea,* and *Cyrtophora,* but its significance is unknown).

The distribution of these postures among 22 species of orb-weaving uloborids is given in Table 1. With two exceptions (*Uloborus* 2072 and *U. conus;* Lubin et al. 1982), it appears that within a genus the resting posture is consistent.

DISCUSSION

The function of constrained postures (B, C, D) is probably one of outline concealment, serving to hide the outline of the legs and make them appear part of a single



Figs. 1-2.–*Tangaroa beattyi* Opell female: 1, ventral view; 2, lateral view. Figs. 3-4. *Octonoba octonaria* (Muma) female: 3, ventral view; 4, lateral view. Figs. 5-6. *Zosis geniculatus* (Olivier) female: 5, ventral view; 6, lateral view.

structure, thus reducing predation (e.g., Robinson 1969a). The spiders' consistent use of the relatively exposed orb hubs as resting sites (Eberhard 1969), their production of stabilimenta (thought to be camouflage devices—Eberhard 1973), the disruptive coloration of their legs (e.g., Figs. 3-12), the presence of setal brushes on tibia I of *Uloborus* species which hold legs II beside tibia I (Figs. 7, 8), and the irregular outline of the abdomens of some species (e.g., *Uloborus* 2073) are all in agreement with this crypsis hypothesis.

Four lines of evidence suggest that posture A is plesiomorphic (= ancestral) with respect to the others: 1) this is the posture of *Tangaroa*, a genus whose morphology shows it to contain the most primitive living uloborids (Opell 1979); 2) similar stances are found in other web-building spiders (e.g., Araneidae, Dictynidae, Tengellidae, Agelenidae, and Dipluridae, personal observations); 3) this posture is assumed at night by at least some species (e.g., *U. diversus*, Eberhard 1973) and occasionally is assumed at both day and night by others (e.g., *P. vicina*) which usually adopt other, apparently cryptic postures during the day; and 4) all orb-weaving uloborids we observed assumed this posture in response to prey contacting the web when it seems to be important for prey location and evaluation.

Three morphological modifications appear to be associated with posture C: 1) Dense, distal tibial setal tufts (Figs. 7, 8) which hide the tips of the second legs, or conceal the outline of the legs, or both (perhaps equivalent to "decorations" on the legs of some mantids, walking sticks, and other insects); 2) narrowed cephalic carapace region which, at the level of the posterior lateral eyes is 0.62 maximum carapace width (mean for *U. glomosus, U. metae, U. trilineatus*), as opposed to 0.86 in *Tangaroa*, (mean for *T. tahitiensis* and *T. beattyi*), 0.77 for *Zosis*, (mean for *Z. geniculatus* and *Z. peruvianus*), 0.67 in *Octonoba octonaria*, 0.67 in *Conifaber parvus*, and 0.69 in *Philoponella* (mean for *P. fasciata, P. republicana, P. vicina, P. vittata*), and 3) first femora which bow retrolaterally in the proximal third of their length to accommodate their distal appression while allowing pedipalpi to extend between their bases (Fig. 7). More careful comparison will no doubt show other less conspicuous modifications that, in conjunction with 2 and 3, allow legs I to extend directly forward.

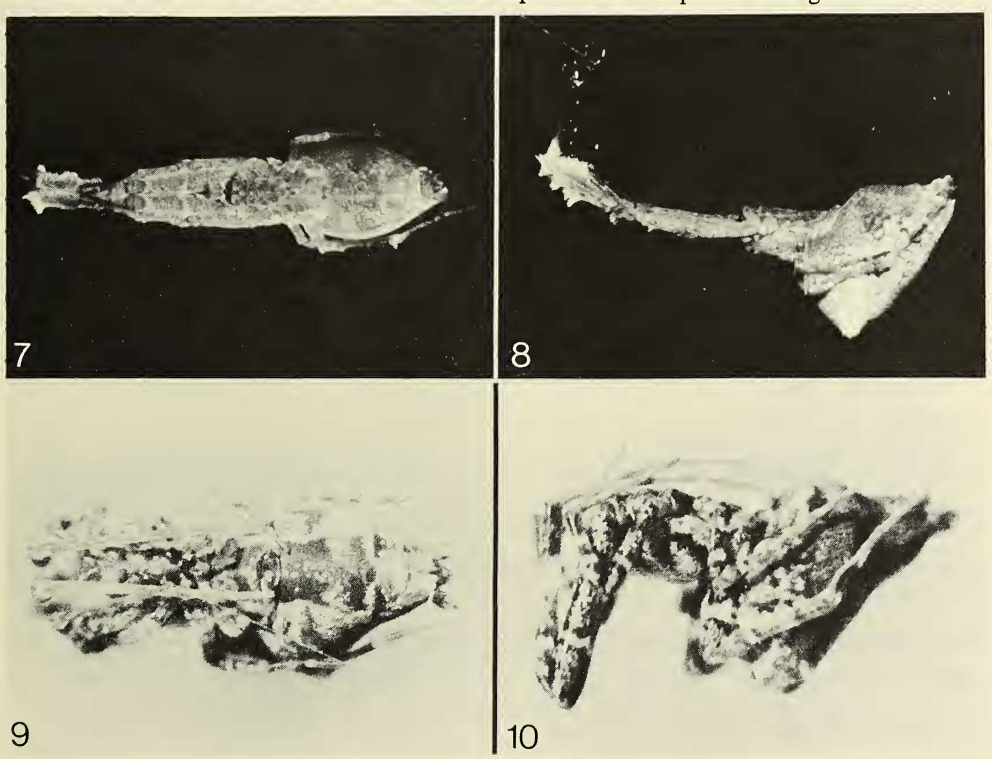
Posture C may represent a linear special protective resemblance similar to the stick mimicry attitudes assumed by some phasmids. In describing these postures Robinson (1969a, b) points out that, in addition to allowing protraction and opposition of anterior legs, adaptations similar to 2 and 3 above conceal the head and antennae, making the insects more linear in appearance. This closely parallels the situation in *Uloborus*. Although the first metatarsae and tarsae bend abruptly upward, their dark color contrasts with the lighter proximal segments and visually truncates the legs at the tibial tufts (Figs. 7, 8), maintaining a more linear appearance. In darkly pigmented *U. glomosus* the same effect is achieved by dark tibial setal tufts and light metatarsae and tarsae.

Some *Miagrammopes* species also possess distal tibial setal tufts which contribute to their cryptic appearance. It is not clear whether these tufts are homologous with those of *Uloborus*, but this would be consistent with Opell's (1979) phylogenetic proposals. Their function is probably somewhat different, however, as *Miagrammopes'* first legs are quite long and the spiders' second legs extend only to the patellae (Lubin et al. 1978, fig. 9) and, therefore, do not rest in the setal tufts as they do in *Uloborus* which rest in an extended cryptic posture. The setal tufts may obscure the outline of the first leg, but they do not hide the tips of the second legs. Perhaps this was the original function of these tufts, and their use in conjunction with posture C evolved later.

Crouched posture D contrasts with C not only because legs I and II are drawn close to the body (Figs. 9, 10), but also because legs II rather than legs I are responsible for the spider's anterior purchase on the web. Other than coloration, no morphological modifications appear to accompany this posture. In contrast to cryptic posture C, posture D may be a eucryptic device which, along with the darker color of many *Philoponella* species, renders the spider inconspicuous against its background rather than making it appear as a piece of debris. Although there is no evidence in *Philoponella* for the background selection which Robinson (1969a) lists as characteristic of eucryptic animals, *Philoponella* commonly construct webs in buttress roots of trees, on steep banks, and on rock outcrops where the background is dark. A pair of light paraxial ventral abdominal stripes usually bridge a small gap in one or more linear stabilimenta which cross the hub, further contrasting the spider and its web and helping it blend with its background.

It may be advantageous for species which are facultatively colonial, as are most *Philoponella* that have been studied (Eberhard 1969, Lahmann and Eberhard 1979, Lubin 1980, Muma and Gertsch 1964, Opell 1979), to be inconspicuous (eucryptic) rather than to exhibit protective resemblance. A number of relatively evenly spaced, suspended pieces of apparent debris might elicit further investigation by a predator and would almost certainly encourage learned recognition.

These resting postures support division of the traditional genus *Uloborus* into a number of morphologically distinct genera (Lehtinen 1967, Opell 1979) and aid in their field identification. The cryptic posture of *Uloborus* serves as an additional autapomorphic (= derived) character for most members in this genus. The more generalized posture of *Octonoba* also indicates that the *Uloborus* posture is unique to that genus and is not



Figs. 7-8.–*Uloborus trilineatus* Keyserling female: 7, ventral view; 8, lateral view. Figs. 9-10. *Philoponella vicina* (O. P.-Cambridge) female: 9, ventral view; 10, lateral view.

present in its sister group. *Zosis* posture appears derived from a generalized posture of the *Zosis, Octonoba, Conifaber* lineage. Morphological characters suggest that *Conifaber* is more closely related to *Zosis* and *Octonoba* then to *Philoponella* and its apparent postural similarity to the latter is the result of convergent evolution. Our observations of *Conifaber* were unfortunately not detailed enough to determine whether its posture is identical in every detail to that of *Philoponella.*

The occurrence of posture D in two cone-weaving *Uloborus* species (*U.* 2072 and *U. conus*) is difficult to interpret. Only brief observations were made of a single individual of

Table 1.—Daytime resting postures assumed by orb-weaving uloborids.

SPIDER	POSTURE
Tangaroa	
beattyi Opell	A
Octonoba	
octonaria (Muma)	A
varians (Bösenberg and Strand)	A*
Zosis	
geniculatus (Olivier) - American	B
geniculatus (Olivier) - Indian	B
peruvianus (Keyserling)	B+
Uloborus	
diversus Marx	C
glomosus (Walckenaer)	C+
trilineatus Keyserling	C & C+
eberhardi Opell	C
segregatus Gertsch	C
sp. (2073)	C
sp. (2072)	D
conus Opell	D**
Conifaber	
parvus Opell	D++
Philoponella	
arizonica (Gertsch)	D++
oweni (Chamberlin)	D++
para Opell	D++
republicana (Simon)	D
semiplumosa (Simon)	D
tingena (Chamberlin and Ivie)	D
vicina (O. P.-Cambridge)	D
vittata (Keyserling)	D

*From a photograph in Yoshida (1980). Due to variability in postures (see text), this characterization is only tentative.

+The spider held legs I and II pressed more or less together and directed forward, with III and IV close to the body, but it was not noted whether legs II held the web or not.

**Lubin et al. (1982).

++The spider definitely crouched, and its front legs were not extended anteriorly, but details of the posture were not determined.

U. 2072 and it is possible that this species may exhibit other resting postures. Both species have two morphological characters (narrow cephalic region and setal tufts on the first tibia) associated with posture C. If our functional interpretations are correct, these modifications would not evolve unless the spider already assumed a posture similar to C, so it appears that at least in this genus posture D is derived from posture C.

Thus posture D may have evolved three times in the Uloboridae: in *Conifaber*, in *Philoponella*, and in some *Uloborus* species. This apparently unattractive conclusion is nevertheless the best possible with our present data, since, if resting posture is used along with the morphological characters presented by Opell (1979), this scheme is still the most parsimonious. It is worth noting that *U. diversus* sometimes assumes a posture similar to D but with the front legs folded dorsally rather than ventrally over the cephalothorax. (fig. 3, Eberhard 1973). This posture is never used at the hub, but is sometimes assumed when the spider is alarmed and jumps from its web. It seems likely that this represents an independent derivation of the "crouching" outline which, as with posture D, hides the spider's legs.

As with many other features of uloborid biology, resting postures show striking similarities with orb-weaving spiders of the family Araneidae. The araneid *Azilia* sp. rests on its orb in a posture similar to C except that the tibial-metatarsal angle of the first leg is larger than 90°, and the spider assumes a posture similar to D after falling to the ground when disturbed.

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